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Patterns of animal distribution on the African Continent (summing-up talk)

We are having this symposium at a time when most profound changes are going on around us, changes which affect society, but which also affect the nature, the fauna and flora in particular. The natural conditions of life are destroyed, and a new order or disorder prevails in their place. Indigenous animals and plants are disappearing from the countries in which they used to be found. Take our cities, or for that matter, the cities in any civilized country. Whatever animal and plant life is left in the cities is of foreign origin: the trees are all exotic, the flowers in the gardens are predominantly so, the animals are by and large gone altogether except for a very few. But even if we turn to the platteland, the picture is not essentially different. Cultivated crops are introduced: mealies, wheat, sugar cane . . . The trees are exotic: European willows, Australian acacias. Even the weeds are foreign: khakibos, cosmos, jointed cactus, prevail. In the forestries we see stands of eucalyptus and pine. In ranching areas more of the natural vegetation is left, but the larger animals are gone to a very great extent. The pattern of animal and plant distribution built up in hundreds of millions of years, is being destroyed almost in the living memory of one generation of men. The peculiar distinctions of different countries are disappearing, and a homogenized and impoverished fauna and flora are taking their place. As Elton (1958) puts it, we are attending at a breakdown of Wallace's Realms—the great zoogeographic areas which used to be so distinct from one another.

Under the circumstances it is the first duty of zoogeographers, or perhaps of biologists in general, to make a concise recording of the present state of the distribution of animals and plants, a recording of conditions which will not be discernible much longer. Once they go, getting information about the past conditions of life on this planet will be practically impossible. For this reason I should like to commend with the greatest satisfaction the work that has been performed by our mammalogists, who have made a detailed survey of the distribution of large mammals in the four provinces of the Republic of South Africa and in South-West Africa. (See papers by Bigalke and Bateman, p. 85, Vincent, p. 110. Kettlitz, p. 118, van Ee, p. 53, van der Spuy, p. 41). The work on small mammals, as reported in further two papers (Davis, p. 56, Meester, p. 77) is catching up with that done on larger animals. The work on the distribution of birds seems to have been carried out in great detail, so that the three speakers on bird distribution have not so much reported new observations, but have sought to correlate the already known distribution with certain factors of climate, vegetation, barriers presented by river valleys, etc. The present distribution of lower verte-

brates seems to be known quite accurately, as can be judged from papers dealing with amphibians (Poynton, p. 252) and fishes (Crass, p. 229, Farquharson, p. 233, Jackson, p. 223). Needless to say, the surveys of animal distribution should be repeated periodically, so that we can be aware of any further changes that are taking place. The state of affairs in respect of invertebrates is not quite as satisfactory. In respect of some groups the information available is fairly complete, but other groups still have not been worked on systematically. Fortunately the lower animals are less affected by the activities of man, and there is still time to make exact records in most cases.

This most urgent task having been performed, inevitably we turn from the registering of facts to the underlying causes. We ask ourselves the great question: why? Why are the animals and plants distributed over the world as they are, or perhaps, as they used to be before the activities of man have thrown everything into a turmoil?

To understand how the animals and plants have become distributed as they are, we cannot do better but to try and study the processes of dispersal of animal and plant species at the present time. In a general way all would agree, that the area occupied by any species is the result of the balance or equilibrium between the tendency of each species to broaden their area of distribution and certain factors which could be referred to as the "environmental resistance". Let us examine these two aspects of animal distribution. I will first deal with the tendency to dispersal.

Random movements of animals must inevitably bring some individuals of a species beyond the area in which the species is established. How far, and how fast can such individuals go? Obviously the movements of dispersal are only indirectly related to powers of locomotion. We know that some birds can cover enormous distances in a matter of a few weeks during their seasonal migrations, but nevertheless keep to restricted areas, and the migrations themselves are limited to fairly narrowly specified routes. On the other hand it is known, that some animals systematically migrate beyond their established areas, even if they cannot survive in the territories they reach, so that their journey is one of no return. It is reported (Ford 1953) that some butterflies such as the Red Admiral *Vanessa atalanta*, and the Painted Lady *Vanessa cardui*, are regularly found in England, although they cannot survive the British winter. Every year in spring they fly across the channel from the Continent.

Specialists in various groups will certainly recall other cases of this kind. I personally have observed something similar with dragonflies in South Africa. In the years from 1950 to 1959 I have kept under very close observation an area on the outskirts of Johannesburg, mainly because I used the pools and small dams scattered in the area as a source of frogs' eggs and embryos for my embryological work, but also in connection with my study of the dragonfly fauna. I came to know the area very well. I was therefore very thrilled one day in March, 1954, to find on one of the pools several specimens, ♂♂ and ♀♀, of a minute dragonfly of the genus *Agrioctenemys*. The next year I specially searched the area for further specimens of *Agrioctenemys*. None were to be found on the same pool, but in February 1955, I caught 1 on another pool some 500 yards from the first. I have never seen this dragonfly again near Johannesburg, in spite of careful searching. The nearest place I know where the species occurs in abundance is on the Magalagala River near Potgietersrust. What apparently happened, was that some specimens (or possibly even only one ♀ of *Agrioctenemys*, which is a very poor flier) were carried by the wind to Johannesburg. A colony was founded here, which persisted at least two years, but did not get established and disappeared.

An analogous case occurred in October 1957, when I observed in the same area a specimen of another dragonfly *Rhyothemis semihyalina*. This is a very conspicuous dragonfly, with black proximal parts of the wings. In flight it is easily recognizable and cannot possibly be overlooked. In the course of a few days I observed several of these dragonflies flying along the pools in my area. They were never seen either before or after. The nearest place where

the species occurs regularly is also the Magalagu River near Potgietersrust. In this case the dragonflies must have reached Johannesburg, which is far outside the normal range of the species, by active flight, but they failed to establish a colony, as I would certainly have been able to notice their presence in subsequent years had any developed in my pools.

The conclusions that I wish to draw from observations of this kind is that animals will always be found wandering beyond their established range of distribution, and as a rule these wanderings will lead to no permanent effect; the migrants failing to settle permanently, and dying off either immediately, or after a few generations.

We know, however, that under certain circumstances species do increase their area of distribution, and populate areas where the species had not been found previously. It is of importance in connection with the present discussion to know the approximate rates of dispersal of such species. Observations are available in respect of exotic species introduced by man into overseas countries. I would like, however, to quote two examples of the spreading of the area of distribution of species in their own native country. Several British butterflies have shown fluctuations in their area of distribution. Around the beginning of this century they were found only in the south-western counties of England, but later made a recovery and spread out to the north and east (Ford, *loc. cit.*). The Comma *Polygionium C-album* extended its distribution to the east between 1915 and 1953 by about 110 miles, that is about three miles per annum. Almost at the same time, between 1920 and 1953, the White Admiral *Limnitis camilla* extended its distribution to the north by almost 60 miles, that is about one-and-a-half miles per annum. These observations are valuable because they more directly illustrate what may be the rate of distribution of species under perfectly natural conditions.

As I have said, there are many records of the dispersal of species brought into new countries from overseas. The Gipsy Moth *Limantria dispar* was introduced from Europe to North America and in 25 years it spread 220 miles to N.N.W. from Boston where it was brought originally, an average of about nine miles per annum. (Quoted from Elton, 1958). The Muskrat *Ondatra zibetica* was brought from the United States to Bohemia in 1905, and after 25 years spread over an area with a radius of 180 miles, an average of eight miles per annum (Elton, *loc. cit.*). Turning to our own country, I should like to quote the following examples: The Indian Myna *Aeridotheres tristis*, introduced into Durban about 1900 (Bigalke, 1936), reached Johannesburg before 1950, having made 400 miles in under 50 years which makes the rate of dispersal about eight miles per annum. The European Starling *Sturnus vulgaris*, brought to Cape Town about 1900 (Bigalke *loc. cit.*), is said to have reached Port Elizabeth in 1956 (Macnae, 1961)—an average rate of dispersal of about eight miles per annum. A similar rate of dispersal has been observed in the case of the English Sparrow. Lastly, the American Grey Squirrel *Sciurus carolinensis*, released near Cape Town in 1900, spread to an area with a radius of 40 miles by 1948, increasing its area by about 0.8 miles per annum (Davis, 1950).

The above data show how fast a species can spread when the environmental resistance is reduced or absent. Let us compare this speed—the potential rate of dispersal of species—with the periods available for the establishment of the present pattern of distribution of animals in Africa. It is usually assumed that most of the species living at present on the African continent have come to be where they now are in the course of the Pleistocene, that is during the last 1,000,000 years. The African continent is, roughly, 5,000 miles from north to south. Now, if any species spread its area at the rate of the Indian Myna or the Gipsy Moth, it would cover the whole continent in 600 years. If the dispersal were at the relatively very slow rate of the grey squirrel the continent would be fully occupied in 6,000 years. To cover the whole continent in 1,000,000 years it is only necessary to proceed at an average speed of eight yards per annum—a rate probably within the reach even of soil mites!

What emerges from these considerations is that the powers of dispersal of animals over

the surface of the earth are quite out of proportion to the time available; and that, if any of the indigenous species were capable, under existing conditions, of increasing their area of distribution, they would have done so long ago. The present pattern of distribution is therefore a *stable* one, or rather it is one of dynamic equilibrium, which is characterized by continuous attempts of animals to disperse more widely and the impossibility, under present circumstances, of getting a foothold anywhere outside their established areas of distribution. This does not apply to newly introduced species or to some indigenous species which are now moving into new environments created by man.

We must now consider the nature of the factors which contain the majority of indigenous species in their present areas of distribution. A very important and much used concept is that of "*barriers*"—obstacles which supposedly prevent the actual spread of certain animals across them. Some such barriers have been discussed in the present symposium. The most efficient barrier, it seems, is the one preventing fresh water fishes from spreading from one river system into another, even an adjacent one. This difficulty might explain the extreme poverty of the fish fauna in the southern Cape Province, although further north it is much richer, and presumably at least some of the species would have been able to live in the river systems of the southern Cape, if they could get there (Crass, p. 232, Farquharson, p. 249). Even waterfalls seem to be effective physical barriers for fish (Jackson, p. 227, Crass, p. 231). In the well documented paper by Benson, Irwin and White (p. 155) it has been shown that river valleys and rifts have served as barriers for the distribution of some species of birds. These barriers are, however, of a somewhat different kind: Mr. Irwin in presenting the paper has made it clear, that he did not suggest that birds never cross the barrier. This isolation is therefore not absolute. Evidence of the degree of isolation is provided by the existence of different subspecies of birds on the two sides of the valley. To evaluate what this means we should apply the conclusions drawn from the mathematical analysis of natural selection, worked out by Fisher, Sewall Wright, Haldane and others. Wright, in particular (1940), has calculated that, given an average level of selection pressure, genetic differentiation of two populations is not prevented by an exchange of 0.1 per cent of the population in one generation. It is thus quite possible that the subspecific differentiation has been going on in spite of a moderate gene exchange across the barrier.

In most cases of species distribution the border of the area is not delineated by any physical barrier at all: the animals are free to migrate, and the factors holding a species back are those which make it impossible for it to survive and reproduce. These factors are partly abiotic: temperature, moisture, nature (chemical and physical composition) of the soil; and partly biotic, including competition with other species. This seems perhaps elementary, but some important conclusions arise directly from the above. If animal distribution were dependent mainly on physical barriers, large numbers of different animals would have common boundaries of distribution. But if the border of the area occupied by a species is dependent on ability for survival, then each species will be fenced in in a different way. The conditions of survival are extremely differentiated for different species. Furthermore, the borders of the areas under these circumstances cannot be stable: they must be likened to a wavering line, that surges back and forth like the front in a battle, depending on fluctuations in environmental conditions and on changing population pressure inside the area. The survival of any species, depending as it does on innumerable, sometimes very subtle, circumstances, will only rarely be determined by one single factor of the environment. We have heard at this symposium (Liversidge, p. 148), that the same species of birds may be found in different habitats depending on the climate. A factor, such as vegetation, which may be limiting distribution in one combination with other factors, will not have the same effect in a different context.

Due to the intrinsic difference between species, the environment for each is not the same as for any other. The distribution pattern of any species is therefore essentially unique and

unrepeatable. Nevertheless it is true that some patterns of distribution show a closer resemblance than others. The reason is either that the one species is dependent on another, or that they are both dependent on some special configuration of environmental factors, into which a number of species fit as their organic components. If we want to make sense of distribution in animals, we must try to discern such complexes, which, naturally, must encompass the plants as well as the animals. With the maze of individual specific distributions superimposed over one another, large groupings would be easier to characterize than small ones.

In the course of this symposium, reference has often been made to tropical and temperate components of the African fauna. Obviously "tropical" cannot be taken to mean "enclosed between the two tropics, Cancer and Capricorn". The term becomes meaningful if it is applied to a certain complex, defined by geographic, climatic and biotic characteristics. It must be recognized, at this stage, that the geographic tropical and even equatorial zones are not homogeneous in respect of climate, flora and fauna but show a differentiation in two main components. The two components are: the wet tropics, the tropics of the equatorial rain forest; and the dry tropics, the tropics of savanna merging into semidesert, as it is found in N.E. Brazil, and in Africa in Somaliland, where semidesert or desert conditions are found close to the equator. The two biotic spheres are profoundly different.

I do not have time to emphasize the difference in the conditions of life in the tropical rain forest and in the savanna, it will be enough to mention that the overwhelming majority of large African ungulates inhabit the savanna, whilst only a few large mammals, the elephant, the buffalo, and the okapi (replacing the giraffes of the savanna), are found in the tropical rain forest. The birds of the rain forest and the savanna are also, I understand, profoundly different, having but relatively few species in common.

The reason for the existence of arid zones close to the equator is not dependent entirely on the amount of rainfall, but to a large extent on the distribution of rain through the year. In the rain forest zone the rainfall is distributed throughout the year, the earth is always moist, the trees are evergreen and the animals are permanently protected from fluctuations of moisture and temperature. Towards the eastern edge of the African continent, however, the rainfall is seasonal. There is a period during which there is no rainfall, or very little. In Map I I have indicated the areas which, during at least three consecutive months a year, have less than 10 m.m. rainfall per month (the data are compiled from C.C.T.A. maps of monthly rainfall). For three months at least the zone indicated on the map is in a state of drought which may be more or less acute, depending on the absolute figures of rainfall. In this zone the trees lose their leaves during the dry season. Without the protection of the leaves, the soil is exposed to the scorching rays of the sun, and at the same time the fluctuations of temperature, annual and diurnal, become much greater than in the rainforest areas. Conditions for animal life become much more severe. From the map we see, that the drought zone extends without interruption from the western Cape and South West Africa to the Somali peninsula. The vegetation along this "drought corridor" varies from dry forest to open savanna, bush, grassland, semidesert and desert at the ends. The rainforest in the main lies west of the corridor, but on the eastern side of the continent there are patches of rainforest near the seashore and on several outcrops of mountains especially along the Rift valley.

It is obvious that the savannaland—or dry tropic—components reach far into southern Africa. The large antelopes, zebra, and giraffes are animals that thrive all along the drought corridor. The Impala occurs all the way from Transvaal (and formerly even from the northern Cape—Bigalke, p. 95) to Somaliland. To give an example for a completely different group of animals: the Neuropteran genus *Silveira* is distributed along the dry zone from S.W. Cape and South West Africa across Rhodesia to Katanga (Tjeder, 1960).

At its south western end the "drought corridor" merges into the semidesert and desert region of the Kalahari, and the Namib desert. This end of the corridor whilst closely linked



Map I. Map of Africa showing (stippled) the areas in which the rainfall is less than 10 mm. per month in at least three consecutive months. (Compiled from the CCTA maps of monthly rainfall).

to the more northern parts has developed a peculiar fauna of its own. The zone is clearly characterized by its bird fauna, as has been indicated by Winterbottom (p. 152). It has a characteristic contingent of lizards: 51 per cent of all lizards in South Africa are endemic for the south-west arid zone (Poynton, 1961); and it has 40 species of Solifugae (arachnids adapted to dry conditions) whilst Natal Zululand has seven species (Lawrence, 1953). However the most diversified and abundant component of the arid south west are the tenebrionid beetles, represented in the Namib desert by not less than 35 endemic genera with hundreds of species (Koch, 1960).

PATTERNS OF ANIMAL DISTRIBUTION ON AFRICAN CONTINENT



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|-------------------------------|---------------------------|----------------------------|
| ■ <i>Acanthagyna africana</i> | ■ <i>A. nigrieriensis</i> | ★ <i>Zyxomma atlantica</i> |
| ● <i>A. hispana</i> | □ <i>A. schultzei</i> | ● <i>Z. flavicans</i> |
| ○ <i>A. bullata</i> | ○ <i>A. sextans</i> | |
| ■ <i>A. cylindrata</i> | ○ <i>A. usnebarica</i> | |
| ★ <i>A. flaviceps</i> | ▲ <i>A. vesiculata</i> | |
| ★ <i>A. immaculifrons</i> | ● <i>A. villosa</i> | |
| ● <i>A. manderica</i> | ▲ <i>A. sulzensis</i> | |

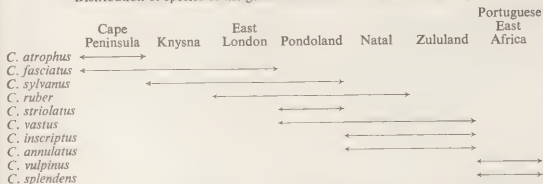
Map II. Distribution of the tropical genera of dragonflies *Acanthagyna* and *Zyxomma* in Africa.

Let us now consider the wet tropics. Do components of the wet tropics reach into southern Africa and, if so, are they related to the wet tropics to the west of the drought corridor, or only to the wet tropics along the eastern edge of the continent?

I should like to present here some data on the distribution of two genera of dragonflies, *Zyxomma* and *Acanthagyna* (Map II, based mainly on Martin, 1908–1909, Schouteden, 1934, and Pinhey, 1961). *Acanthagyna* is a circumtropical genus of dragonflies found in tropical America, East Indies, India and central Africa. The dragonflies belonging to this genus have very peculiar habits. The insects are crepuscular, fly at dusk, after sunset, and during daytime hide amongst the densest foliage. They are typical rainforest insects, though they are also found in the tropics in dense groves of bamboo (Fraser, 1949). Sixteen species are found in Africa, mainly in the Congo and adjoining territories, but also in patches of rainforest around the rift valleys and on the Indian Ocean coast. I have been able to trace three species of *Acanthagyna* to Zululand (Richards Bay) (Balinsky, 1961) and one species even as far as Port St. Johns (Balinsky, 1958). The genus *Zyxomma* has a similar mode of life, and practically the same distribution: from West Africa, through the Congo basin to Zululand (Balinsky, 1961). These data, which I know from my own experience, satisfy me that components of the western tropical rainforest fauna are in fact to be found on the eastern coast of South Africa. The distribution of other animals, in particular of the amphibians as analysed by Poynton (1960, and p. 252) fall into a similar pattern.

We are thus faced with a most interesting situation, whilst animals of the savannaland and arid areas show close relationships in a zone reaching across the continent from the south-west to the north-east, rainforest animals are distributed right across the "drought corridor" from the north-west to the south-east. It is true that in the area of the great lakes there are several patches of rain forest, mainly on mountains, which could serve as stepping stones for the movement of animals from the north-west to south-east and *vice versa*. At present, however, there are considerable areas of open country between the patches of rain forest. The difficulties can probably be explained away if we take into consideration the fluctuations of climate and the displacements of vegetation zones, as these have been indicated in the papers presented by Cooke (p. 11) and van Zinderen Bakker (p. 16). During cold and wet periods the rain forests must have expanded and closed the "drought corridor" completely or at least narrowed it still further, enabling the animals of the wet tropics to migrate from west to east (and from east to west). During hot and dry periods, the drought corridor would have expanded allowing Kalahari and even desert conditions to surge in, linking more closely the arid south-west with the Somaliland arid area, thus accounting for the close links in the fauna of these areas that have been pointed out by Winterbottom for birds (p. 152), Davis for small mammals (p. 56) and Theiler for the tick *Ornithodoros savignyi* (p. 212). The opening and closing of the "drought corridor" may have occurred repeatedly. What I said earlier on the potential rate of dispersal of animals proves that they could make full use of such fluctuations in the environment.

I now come to the last zone—the temperate zone. There is no dispute that in the south of the continent there are found numerous species, genera and even families of animals that do not occur further north. The question that we have to answer is whether these forms constitute a separate fauna, a unit which is distinct, as a whole, from the other complexes of forms on the African continent. To make this question more meaningful, I should like here to point to the very frequent occurrence of groups of closely related species distributed over a large area in such a way that either the species replace each other, or that areas of distribution of neighbouring species overlap partially. To illustrate this type of distribution I will quote the example given by Lawrence (1953) relating to species of the millipede genus *Chersastus*.

Distribution of species of the genus *Chersastus* after Lawrence (1953)

This example shows that it is dangerous to characterize faunal units by the presence of a species, without considering the distribution of closely related forms. Although, in this example, *Chersastus atrophus* would appear to be a Cape endemic, it is obvious that as a group, the species of *Chersastus* are more widely distributed; and the local differentiation in the Cape is not essential and deserves but little attention.

If it is thus desirable to check whether there is an independent temperate fauna in Africa, attention should be given to those organisms that have no closely related forms in the rest of the continent. If this criterion is made, it at once becomes evident that such a group of organisms in fact exists. Moreover, it becomes clear that these organisms constitute a distinct complex. It is the "palaeogenic fauna" that has been demonstrated in the paper given by Stuckenberg (p. 190). To this complex of animals belong some insects with aquatic larvae, such as the dragonflies of the genus *Chlorolestes*. These extend from the western Cape through the Drakensberg mountains to the Transvaal escarpment (Woodbush) and to the eastern Southern Rhodesian escarpment—Ingha Mountains. To the same complex belong the stoneflies of the subfamily Notonemouridae, the distribution of which extends as far north as the Transvaal escarpment (Woodbush). Both these groups of animals have Gondwanaland affinities. The genus *Chlorolestes* is closely related to the Australian genus *Synlestes*, and the family Notonemouridae, in addition to South Africa, is found in Madagascar (Paulian, 1949), the Tierra del Fuego in South America, and in Australia and New Zealand (Evans, 1959). I should also like to mention the frog genus *Heleophryne*, found in the Cape and in the Drakensberg mountains, a representative of the family Leptodactylidae, which is mainly South American and Australian. It is most remarkable that the tadpoles of *Heleophryne* are specially adapted to life in mountain streams. These frogs thus belong to the same biotic complex as the dragonflies of the genus *Chlorolestes*, and the Notonemourid stoneflies!

The South American and Australian affinities of the "palaeogenic fauna" have been stressed by Stuckenberg (p. 193) and of course it is known that the flora of the South Cape has the same affinities, the families Proteaceae and Restionaceae being found only in the southern hemisphere in South America, southern Africa and Australia. Affinities are also unmistakable, as is evident from fossil remains, to the Antarctic Continent.

The occurrence of common or closely related faunal and floral elements in the continents of the southern hemisphere has been one of the arguments for the existence of land connections between these continents, as postulated by the theories of continental drift (Wegener, du Toit). They were part of one whole—the Gondwanaland. The theory of continental drift had come into ill repute and had been emphatically rejected by many zoogeographers (see Darlington, 1957). In recent times, however, new facts have been discovered which put the

whole matter in a new light. The new data come from a study of so called palaeomagnetism. It appears that when rocks are being formed, either by sedimentation, or through solidification of volcanic lavas, the rocks become magnetized in conformity with the prevailing orientation of the magnetic forces at the time of their formation. If the rocks of a known age are studied, it is possible to determine the orientation of the magnetic forces during a certain period of the earth's history, and thus deduce the position of the magnetic pole at that time.

Studies of this kind have shown that the magnetic pole in ancient periods of the earth's history was not in the same position as it is now. The most astonishing fact revealed is, however, that determinations made in different parts of the world indicate different positions of the pole. This can only mean that at any given time the relative positions of the continents in respect of the magnetic poles were not the same as they are now. In other words, the continents have actually moved in respect of one another. Continental drift has actually taken place.

A weakness of the theory of continental drift has been previously that no forces were known which could account for the movement of continents. Now this fault is also being eliminated. Two major theories proposed in this connection are that the continental drift is the result of thermal convections in the earth's mantle, which underlies the continents (see Dietz, 1961), or that the earth is actually expanding, bursting at the seams as it were, the seams situated in the midoceanic ridges, with the result that ocean beds broaden, and the continents become disrupted and drawn apart (see Carey, 1958; Heezen, 1960).

From data on palaeomagnetism it is not only possible to deduce that continents have moved, but, with more abundant data available, it will be possible to reconstruct the course of their migrations and their exact positions for any period of the earth's history (Irving, 1958). I may venture a prediction that, within foreseeable future, the state of affairs in relation to continental drift will be completely the reverse of what it used to be. Formerly land connections between continents were adduced by biogeographers to explain certain peculiarities of animal and plant distribution. Now the positions of continents in the past and their movements will be established on an objective basis, as we know the duration of geological periods from uranium and carbon determinations (see Kulp, 1961), and to these data the biologist will have to adapt his theories of animal and plant distribution. It will be possible to make certain predictions. Even now it is possible to make a definite prediction as to the animal fossils which will one day be found on the Antarctic continent.

I will now return to the temperate fauna of southern Africa. It will be seen that this fauna is nothing else but the relict of the Gondwanaland fauna. As the separation of the Gondwana continents occurred presumably some time during the Cretaceous period, the common Gondwanaland elements can only belong to groups which were developed not later than middle Mesozoic. These would be various invertebrates, including arthropods and the more ancient groups of insects. Amongst the fishes the most advanced groups, such as the Cyprinids, are excluded. The frogs evolved in the earlier part of the Mesozoic (see Griffiths, 1956) and therefore could be represented. In this connection the genus *Heleophryne* may well be considered a Gondwanaland element. Modern lizards and snakes probably evolved too late to have been a part of the Gondwanaland fauna, and we have seen that they are not associated with the palaeogenic fauna, but have their centre of speciation in the south western arid zone. Amongst the mammals and birds, only the most ancient groups could have been common to the Gondwanaland continents. It has been suggested that the Ratitae, in spite of established opinion, may after all have been a group of common derivation and of Gondwanaland origin (Evans, 1958).

From what we know it appears that all Gondwanaland continents drifted mainly in a northerly direction, away from the southern pole, Antarctica being an exception, as it moved southwards to its present position (Blundell and Stephenson, 1959). It follows that the climate

over most of Gondwanaland was originally cold to temperate. The adaptation to this type of climate has been preserved to a large extent by animals and plants with southern hemisphere affinities. In Africa we have the greatest development of the Gondwanaland elements in the southernmost tip of the continent, and further north these elements are restricted to the mountain ranges where temperatures are lowered by the altitude. I believe that this is the reason of the otherwise mysterious feature stressed by Poynton (p. 252), namely that whilst degrees of moisture differentiate between animals of recent adaptation, temperature divides faunas of different historical origin. This difference is due to the past existence of the Gondwanaland continent and is not represented in the same way in the northern hemisphere where the fauna and flora of the higher latitudes is not more ancient, but on the contrary more modern than that in lower latitudes. This, of course, in its turn is due partly to Pleistocene glaciation.

In Africa the ancient temperate fauna must have occupied during early Mesozoic a considerably greater part of the continent, and at some stage the present disconnected distribution on mountain ranges may have been linked together. Nevertheless a considerable northern part of the African continent must have reached into the zone with a hotter and possibly more arid climate. The fauna of this zone seems to have merged across the equator with the fauna of *Laurasia* (the present Holarctic) and is not recognizable as a separate unit any longer. Instead it has given rise, on the broad expanses available for their distribution in the northern hemisphere, to the higher forms of life: birds, mammals, modern reptiles, amphibians and fishes, which now figure in the fauna of Africa as the dominant components of the wet and dry tropics, and even of the arid south-west.

The temperate faunal elements were prevented from merging with this stream of modern life by their adaptation to cooler temperatures and by being closely linked together in biotic complexes such as those of mountain streams and evergreen forests of the south, for which the equatorial and subequatorial zones have served through the ages as an insurmountable barrier.

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